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Mass migration and life cycle adaptation – a survival strategy of terrestrial earthworms in Central Amazonian inundation forests*

by

Joachim Adis and Gilberto Righi

Dr. Joachim Adis, Max-Planck-Institute for Limnology, Tropical Ecology Working Group, Postfach 165, D - 2320 Plön, F.R.G.
Dr. Gilberto Righi, Departamento de Zoologia, Universidade de São Paulo, Caixa Postal 20.520, São Paulo 01000, Brazil.
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Abstract

Horizontal mass migration of juveniles towards higher situated dryland areas due to annual flooding of inundation forests in the Rio Negro valley (5 - 6 months) is reported for *Tairona tipema* (Glossoscolecidae). The synchronization of cocoon production in adults which return to the inundation forest with receding flood, the short period needed for the offspring to mature and the acquisition of an annual life cycle are considered biological adaptations which enable inhabitation of an extreme biotope. Vertical mass migration is reported for *Andiorrhinus venezuelanus tarumanis* (Glossoscolecidae) in an inundation forest near the Rio Solimões valley. Animals move from the waterlogged soil to the trunk/canopy area, shortly before annual flooding. Mucus secretion facilitates nocturnal trunk ascents of individuals up to 19 cm in length.

Keywords: **migration, soil fauna, inundation forests, Oligochaeta, Brazil.**

*This study is dedicated to Dr. Hans Klinge (MPI, Plön) to commemorate his 60th birthday.

1. Introduction

Inundation forests in Central Amazonia are annually flooded for 5 - 6 months. JUNK et al. (1988) suggested that the monomodal flood pattern of the Amazon River and of its large tributaries, the flood pulse, is the major force controlling the aquatic and terrestrial biota in Amazonian river-floodplains. Regular flooding certainly resulted in a pronounced seasonality of terrestrial invertebrates of inundation forests in an otherwise "seasonless" environment (ADIS 1984; ADIS & STURM 1987; ADIS et al. 1986, 1988; IRMLER 1981, 1985; PAARMANN 1986; PAARMANN et al. 1982). The periodic loss of the terrestrial habitat is compensated in various ways, such as: (1) invertebrates stay near the waterline and move according to the ascending or descending flood (IRMLER 1979); (2) invertebrates move to non-flooded trunk and canopy areas in the inundation forest (ADIS 1981, 1982; ADIS & SCHELLER 1984; ADIS & MAHNERT 1985; ERWIN 1983; FRIEBE & ADIS 1983); (3) invertebrates move to adjacent dryland biotopes during inundation (ADIS et al. 1986); (4) invertebrates acquire adaptations for remaining in flooded terrestrial areas (ADIS 1986; ADIS & ARNETT 1987; ADIS & STURM 1987; BECK 1969, 1976; IRMLER & FURCH 1979; MESSNER & ADIS 1988; SCHELLER & ADIS 1984; SMITH & ADIS 1984).

In this paper migration modes of terrestrial Oligochaeta prior to forest inundation as well as life cycle adaptations are discussed.

2. Study area and methods

Oligochaeta were collected from 1975 to 1977 and between 1980 and 1988 in the course of ecological studies on Central Amazonian arthropods from inundation forests (comp. ADIS 1981, 1984; ADIS & SCHUBART 1984). Information on the classification of inundation forest types is given by PRANCE (1979).

The first study site was situated on the lower course of the Rio Tarumã Mirĩm (03° 02'S, 60° 17'W), a tributary of the Rio Negro, about 20 km upstream from Manaus. The blackwater inundation forest was situated on a slope and extended from the non-inundated dryland area with a constant decline (< 5 %) to the bare sandy shoreline of the Tarumã Mirĩm River (see profile in BECK 1976). The soil of the inundation forest consisted of clay, silt and sand material and had an organic layer of 5 - 10 cm thickness. Its fine humus was penetrated by a matting of roots and supported up to 3 cm of leaf litter. The lowest part of the study site was covered annually by floodwater between January and September, the central part from March/April to August/September and the upper part between April and August. Further information on the study site is given by ADIS (1981). Oligochaeta were monitored on the forest floor with 32 pitfall traps (cf. ADIS 1981) with lines of 8 traps being installed at different height along the non-inundated forest slope in 1975/76 and 1976/77. In addition, soil samples were taken with a split corer (0 - 10 cm depth) along a transect up to 31 m distance from the water margin during the increasing and receding flood in different years as described in ADIS & BOGEN (1982). Trunk ascents and descents were detected at weekly or biweekly intervals with arboreal photo-eclectors (= funnel traps) on three tree trunks each between January 1976 and March 1977 (cf. ADIS 1981).

The second study site was at Lago Janauarí (03° 20'S, 60° 17'W), situated on a spit between the Rio Negro and the Rio Solimões about 10 km from Manaus, across the river. The region was influenced by blackwater of the Negro River during low water-level and by whitewater of the Solimões River during the high-water period. The study site in this mixedwater inundation forest (cf. PRANCE 1979) was flat

and had no direct connection with non-flooded dryland areas, which were several km distant (comp. Fig. 18 in IRMLER 1975). The soil consisted of clay, predominantly montmorillonite which represented alluvial deposits of the Solimões River. A scanty litter layer was formed during the non-inundation period of about 8 months duration (September - April). It was mostly carried out of the forest by the current of the annual floodwaters. Further information on the study site is given by ERWIN (1983) and IRMLER (1975). Oligochaeta were monitored on the forest floor with 10 pitfall traps during the non-inundation period between September 1987 and April 1988. Trunk ascents and descents were detected in biweekly intervals with arboreal photo-eclectors on one tree trunk each between July 1987 and May 1988.

Both inundation forests studied were subject to a rainy season (December - May: average precipitation 1,550 mm) and a dry season (June - November: average precipitation 550 mm; cf. RIBEIRO & ADIS 1984). The taxonomic work for this paper was done by G. RIGHI, the collection and evaluation of field data by J. ADIS.

3. Results and Discussion

3.1. Horizontal migration

Inundation forests along the Rio Negro and its tributaries are located on a slope which represents the connection between the higher exposed non-flooded dryland area (terra firme) and the lower situated shore line of the river (ADIS 1984; SIOLI 1951). In our study area the distance between the border of the dryland forest and the sandy and plantless bank of the Rio Tarumã Mirĩm was about 450 m (Fig. 2 in ADIS 1981). The terrestrial earthworm *Tairona tipema* (Glossoscolecidae; RIGHI et al. 1976) was found to migrate from the lower part of the blackwater inundation forest (= igapó; cf. PRANCE 1979) towards the dryland forest with increasing water-level from January onwards (ADIS & BOGEN 1982). Throughout this horizontal mass migration animals stayed 16 - 26 m beyond the water margin to avoid being drowned. All specimens examined represented juvenile stages.

At maximum water-level (in June) flood and earthworms had reached the edge of the dryland forest where up to 1,300 animals per m^2 were counted in 6 - 10 cm soil depth. With receding flood (in July) *T. tipema*, now adult, immigrated into the igapó in accompanying the water margin at only 5 - 10 m distance. August and September represented the period with lowest precipitation in the Central Amazon (20 - 25 mm per month; cf. RIBEIRO & ADIS 1984). Therefore, animals presumably tried to stay as close as possible to the water margin to prevent dessication in the rapidly drying forest soil behind them. The limits of minimum and maximum distance were given by soil humidity (< 100 % (= waterlogged soil) and > 30 %; $p < 0.05$) and pH values (> 3.6, $p < 0.05$; Fig. 2 in ADIS & BOGEN 1982). Clitellates were observed to deposit cocoons in the organic layer throughout the horizontal immigration into the igapó. Maximum abundance of adults which reached the lower igapó (end of August) amounted to 635 animals per m^2 in 0 - 10 cm soil depth. Monitoring of horizontal immigration in subsequent years suggests that adult *T. tipema* mostly dispersed to humid places in the inundation forest as for example logs, roots of butressed trees and soil depressions where they subsequently died. No adults were located in the lower forest soil between October and November. Juveniles were found from December onwards, the beginning rainy season, grazing on calyptra of roots in the organic

soil layer. The new generation started migration towards the dryland forest after rising flood had entered the lower part of the igapó (in January/February).

Development of earthworms in non-flooded regions of temperate and tropical zones was reported to last between 9 and 16 months and life span to reach up to 10 years (EDWARDS & LOFTY 1972). Reproduction of clitellates (= cocoon production) is continuous and interrupted mostly by unfavorable climatic conditions due to seasons, as for example cold or dry periods, which may result in aestivation of earthworms (AYRES & GUERRA 1981; EDWARDS & LOFTY 1972). However, a short breeding period was suggested for "marsh-dwelling" Oligochaeta based on data for *Drilocrius* sp. (Almidae) from a swamp region in Paraguay (STEPHENSON 1931). *Tairona tipema* was reported only from inundation forests in the Rio Negro valley (RIGHI et al. 1976). Horizontal mass migration of the entire juvenile population (to escape flooding), the short time for maturing (to secure annual reproduction), the synchronization of cocoon production with receding flood (to maximize time for terrestrial development) and the acquisition of an annual life-cycle (to maintain population density) are considered biological adaptations which enabled *T. tipema* to live in an otherwise uninhabitable biotope.

3.2. Vertical migration

Mass migration was also found for *Andiorrhinus venezuelanus tarumanis* (Glossoscolecidae; RIGHI et al. 1976), an abundant species in the inundation forest of Lago Janauarí, located on a spit between the Rio Negro and the Rio Solimões. This study area was flat and had no direct connection with the dryland area which, characteristic for the central Rio Solimões valley (cf. SIOLI 1984), was several km distant. Thus *A. v. tarumanis* had to climb trees prior to annual flooding. Most animals, all juveniles, were driven out of the waterlogged soil shortly before forest inundation (Fig. 1). Vertical mass migration of terrestrial earthworms has only been known to occur temporarily and is usually caused by heavy rainfalls (DOEKSEN 1967; EDWARDS & LOFTY 1972; GATES 1961). Mucus secretion was observed to be helpful for nocturnal trunk ascents of *A. v. tarumanis*. The migrating individuals, which were up to 19 cm long, normally moved upward by extending the anterior part of their body. They remained in this position until (drying?) mucus somewhat secured the body to the tree trunk. Then they brought up the posterior part of the body which subsequently adhered to the tree trunk and enabled the next upward movement of the anterior body region. Maintaining the overall body curved or somewhat s-shaped, which was observed in some animals, apparently facilitated trunk ascents even more. A mechanical disturbance of individuals during trunk ascents caused them to fall to the forest floor. The high nocturnal humidity of the air prevented desiccation of the body and animals concealed themselves throughout the day in moist places, e. g. under loose bark. It is presumed that *A. v. tarumanis* stays in epiphytes in the trunk/canopy region during forest inundation. A morphological adaptation, however, as reported for *Andiorrhinos planaria* (Glossoscolecidae; MICHAELSEN 1934) which is dorsoventrally flattened like a planaria, has a "creeping sole" and apparently inhabits epiphytes in the Rio Negro valley permanently, was not observed in our species under study.

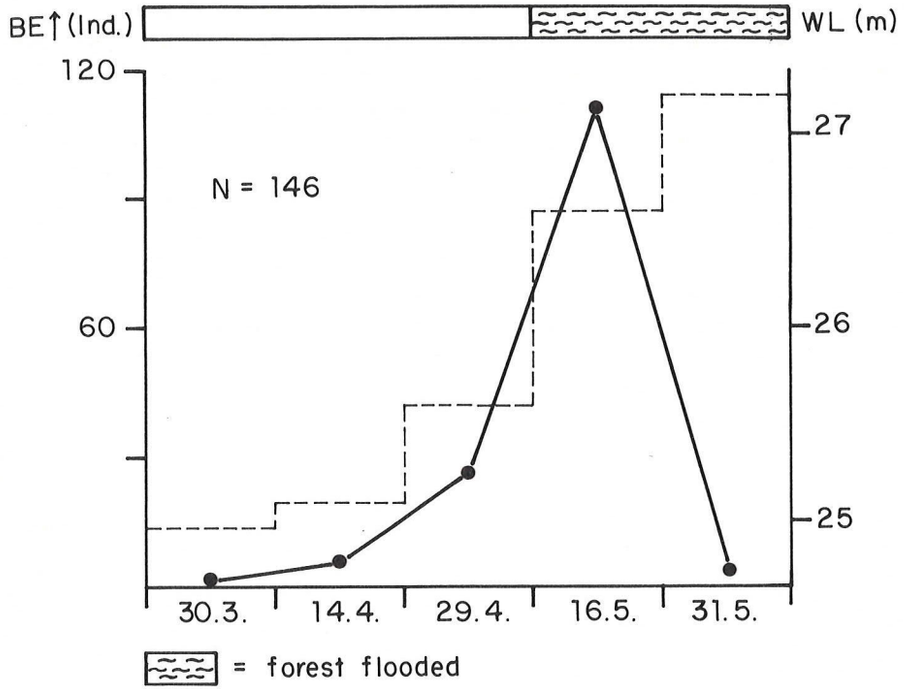

Fig. 1:
Trunk ascent of *Andiorrhinus venezuelanus tarumanis* (Glossoscolecidae) prior to flooding of the inundation forest at Lago Janauarí near Manaus in 1988. Arboreal photo-eclector for upward migration mounted at 3 m height on *Virola surinamensis* (Myristicaceae). Water-level (WL) of the Negro River in the harbour at Manaus (with kind permission of the Port Authorities of Manaus).

A. v. tarumanis was also found in low numbers in the inundation forest at Rio Tarumã Mirím. Its life cycle seems to be similar to that of *T. tipema*. Only juveniles were observed to ascend tree trunks in both areas under study and clitellates were located on the forest floor sporadically with receding flood (cf. RIGHI et al. 1976). Clitellate individuals in related species which inhabited dryland forests were found, however, during the period of rising water-level as well (*A. amazonius, A. caudata*; ADIS unpubl.; cf. RIGHI et al. 1976; NÉMETH & HERRERA 1982). As no specimens of *A. v. tarumanis* were caught in arboreal photo-eclectors for trunk descents in either of the inundation forests under study, it is assumed that animals drop from the trunk/canopy area after the forest had dried.

3.3. Other strategies

Additional survival strategies must exist in other terrestrial earthworm species which were collected in several inundation forests near Manaus (cf. RIGHI 1988, 1989). In *Dichogaster andina evae* (Octochaetidae; RIGHI et al. 1978) only adults were observed to ascend and descend tree trunks and then did so several weeks before inundation forests had been flooded (Rio Tarumã Mirím, Lago Janauarí, Ilha de Curarí at Rio Solimões, cf. ADIS 1981). Juveniles were recorded during the non-inundation period on the forest floor. Juveniles

and adults of *Martiodrilus matapi* (Glossoscolecidae; RIGHI 1969) and adults of *Diachaeta mura* (Glossoscolecidae; RIGHI 1988) were collected at Lago Janauarí during the rainy season in pitfall traps of the non-flooded forest (February to April) but never on tree trunks. These two species may pass inundation on the forest floor as observed for juveniles of *Glyphidrilocrius ehrhardti* (Almidae; MICHAELSEN 1926) which have been found in flooded logs (ADIS et al., unpubl.) and probably use anaerobic respiration via lactic acid (comp. EDWARDS & LOFTY 1972). Ethological and morphological respiratory adaptations were found in Oligochaeta from swamps in Paraguay (CARTER & BEADLE 1931). On the other hand, eggs of Glossoscolecidae can be flood-resistant as reported for terrestrial insects from Central Amazonian inundation forests (ADIS & STURM 1987; ADIS & RIBEIRO 1989; BECK 1976). The ecology of all these species needs to be studied in more detail.

4. Resumo

Migração horizontal em massa de juvenís para áreas mais elevadas de terra firme devido a inundação anual de florestas inundáveis no vale do Rio Negro (5 - 6 meses) é relatado para *Tairona tipema* (Glossoscolecidae). A produção sincronizada de casulos em adultos os quais retornam para a floresta de inundação com a vazante, o período curto da prole para maturar e a aquisição de um ciclo de vida anual são considerados adaptações biológicas as quais possibilitam a habitação de um biótopo extremo. Migração vertical em massa é relatada para *Andiorrhinus venezuelanus tarumanis* (Glossoscolecidae) numa floresta de inundação perto do vale do Rio Solimões. Os animais mudam do solo, saturado por água, para a área do tronco e da copa, pouco antes da inundação anual. A secreção de muco facilita as ascenções noturnas pelos troncos dos individuos com até 19 cm de comprimento.

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